Bull. nat. Hist. Mus. Lond. (Geol.) **52**(2): 109–114 Issued 28 November 1996

The cranial anatomy of *Rhomaleosaurus thorntoni* Andrews (Reptilia, Plesiosauria)

ARTHUR R. I. CRUICKSHANK

Earth Sciences Section, Leicestershire Museums, The Rowans, College Street, Leicester LE2 0JJ; and Department of Geology, University of Leicester, University Road, Leicester LE1 7RH

SYNOPSIS. The skull and lower jaw of *Rhomaleosaurus thorntoni* Andrews, 1922, from the Upper Lias of Northamptonshire, are figured for the first time. New information shows that the external nares are in a perfectly normal position, just in front of the orbits. There is little difference between *R. thorntoni*, *R. zetlandicus* and *R. cramptoni*, the type species of the genus. As they can be considered to be conspecific, *Rhomaleosaurus zetlandicus* (Phillips, *in* Anon, 1854) has priority. *R. zetlandicus* is of more robust construction than the Rhaetian/Hettangian species *R. megacephalus* (Stutchbury, 1846), with, among other differences, teeth having fewer striae and the internal nares of a different construction.

INTRODUCTION

The species *Rhomaleosaurus thorntoni* was proposed by C W Andrews in 1922 for a pliosauroid plesiosaur (Brown 1981) from the Toarcian (Upper Liassic) of Kingsthorpe, Northamptonshire. The type specimen (BMNH R4853) comprises a partial skull, partial mandible and much of the postcranial skeleton, but lacks the limbs. Andrews (1922) described the skull and postcranial remains of the specimen in some detail, but illustrated only the sacral vertebrae and the limb girdles. No illustration of the skull and jaw material exists and it is the purpose of this paper to remedy this omission as part of a series of papers to improve knowledge of the Liassic plesiosaurs (Taylor 1992*a*, *b*; Taylor & Cruickshank 1993*a*; Cruickshank, 1994*a*, *b*). Andrews discussed the characters of his new species, comparing them most closely with those of *R. cramptoni* (Carte & Baily 1863) (NMING F8785). As will be shown below, however, the differences he enumerated between *R. thorntoni* and *R. cramptoni* cannot now be sustained; in addition, many of the characters of *R. thorntoni* are to be found in *R. zetlandicus* (Phillips, *in* Anon, 1854) (Taylor 1992*a*) (YORYM G503).

INSTITUTIONAL ABBREVIATIONS

BMNH	Palaeontology Collections, The Natural History Museum, Cromwell Road, London SW7 5BD (formerly the British Museum (Natural History))
LEICS	Leicestershire Museums, Arts and Records Service, The Rowans, College Street, Leicester LE2 0JJ
MANCH	The Manchester Museum, Oxford Street, Manchester M13 9PL
NMING	National Museum of Ireland, Kilare Street, Dublin 2, Eire
WM	Whitby Museum, Whitby Literary and Philosophical Society, Pannet Park, Whitby, Yorkshire YO21 1RE
YORYM	Yorkshire Museum, Museum Gardens, York YO1 2DR.

SYSTEMATIC PALAEONTOLOGY

Class **REPTILIA**
Subclass **SAUROPTERYGIA** Owen, 1860
Order **PLESIOSAURIA** de Blainville, 1835
Superfamily **PLIOSAUROIDEA** (Seeley, 1874) Welles, 1943
Family **PLIOSAURIDAE** Seeley, 1874
Genus ***RHOMALEOSAURUS*** Seeley, 1874

TYPE SPECIES. *Plesiosaurus cramptoni* Carte & Baily, 1863

Rhomaleosaurus zetlandicus (Phillips, in Anon, 1854)
Figs 1–6

1854 *Plesiosaurus zetlandicus* Phillips, *in* Anon: 19.
1863 *Plesiosaurus cramptoni* Carte & Baily: 160.
1874 *Rhomaleosaurus cramptoni* (Carte & Baily) Seeley: 448.
1922 *Rhomaleosaurus thorntoni* Andrews: 413.
1992 *Rhomaleosaurus zetlandicus* (Anon, *in* Phillips, 1854); Taylor: 52.

DIAGNOSIS. A *Rhomaleosaurus* with a more robust and relatively shorter and wider skull, and a steeper profile of the lower jaw symphysis when compared with *Rhomalosaurus megacephalus* (Stutchbury). Tooth ornament coarse, with widely-spaced ridges and reducing in number towards the tip, triangular in section. Palatal foramina and internal nares lie in the same groove, as opposed to the condition in *R. megacephalus*. The length-width ratio of the snout is 1: 1 as opposed to 1.25: 1 for *R. megacephalus*.

The specimen described here is BMNH R4853. Andrews (1922: 413) did not formally diagnose *R. thorntoni*, except by distinguishing it from *R. cramptoni* in several characters. Andrews (1922: 414) also gave an opinion that *Plesiosaurus megacephalus* Stutchbury, 1846 belonged to the genus *Rhomaleosaurus*, but gave no reasons (see Taylor & Cruickshank (1989) and Cruickshank (1994*a*) for discussion).

Plesiosaurus cramptoni (NMING F8785) is the type species of the genus *Rhomaleosaurus* Seeley, 1874, and comes from Alum

Shales at Kettleness on the north Yorkshire coast (Benton & Taylor 1984) of Toarcian (Bifrons Zone) age. Other English species that have been referred to this genus include *Plesiosaurus megacephalus* Stutchbury, 1846 and *P. propinquus* Phillips, 1854. Only *R. megacephalus* is represented so far by more than one specimen, and it alone seems to be from the Lower Liassic (Rhaetian/Hettangian) (Cruickshank 1994*a*). *Plesiosaurus propinquus* differs from other species in having a marked boss on the hind end of the inner surface of the lower jaw, just in front of the glenoid and in place of the dorsomedian trough (Taylor 1992*a*, *b*), and thus its position within *Rhomaleosaurus* must be reconsidered.

Table 1 Abbreviations used on Figs 1–6.

aiv	anterior interpterygoid vacuity	lgr	lateral groove
		mto	mature tooth
carina	carina on crown of tooth	mx	maxilla
co	coronoid	no	notch
cr	crown	orb	orbit
d	dentary	pal	palatine
dep	depression	palv	primary alveolus
dmfo	dorsomedian foramen	pmx	premaxilla
ec	ectopterygoid	po	postorbital
en	external naris	pt	pterygoid
fac	facial processes of the premaxillae	ptb	pterygoid boss
		ri	ridged ornament on crown of tooth
fan	fan-shaped area		
fo	foramina	rto	replacement tooth
gr	groove	salv	secondary alveolus
in	internal naris	sof	suborbital fenestra
info	foramina associated with internal naris	sp	splenial
		sym	symphysis
j	jugal	v	vomer
		1	position of first tooth

Oblique lining represents broken or sectioned bone or tooth.
Mechanical stipple represents matrix or crushed bone.

DESCRIPTION. *Skull* (Figs 1, 2). The skull and lower jaw have recently been cleaned and conserved, and they alone will be dealt with here. Only the anterior portion of the skull was collected; the clean break surface runs obliquely from a position in front of the left orbit, through the left external naris, to the front edge of the right orbit, and thence through the postorbital bar. Some bone has been lost from the tip of the premaxillae. The right cheek bar is attached to the snout and runs as far as the end of the maxilla. Attached to the cheek bar is a portion of the palate, comprising the right ectopterygoid and a small part of the pterygoid. The base of the postorbital rests on the posterior end of the jugal. Apart from the obvious break, the skull has been damaged by post-mortem effects which have compressed the bone dorso-ventrally and caused the facial processes of the premaxillae to be shortened, so that the midline of the snout has a step, with the posterior part of the premaxillae, as preserved, being pushed under the anterior part and offset to the right. The maxillae may, in addition, have been squeezed together under the facial processes of the premaxillae. All this disruption has obscured the right external naris. In front of, and lateral to, the position of the hidden right external naris, is a deep depression bottomed with crushed bone and an associated wide groove running to the premaxillary edge. The right jugal is partly visible, and is a narrow bone running under the orbit and ending below the postorbital. However, as the bone is heavily pyritized and crushed, and the sutures much closed up, the prefrontal and lacrimal cannot be distinguished. Similarly the detailed structure of the postorbital – jugal area is obscured. There is no reason to believe that this latter region is any different from that described in *R. megacephalus* (Cruickshank

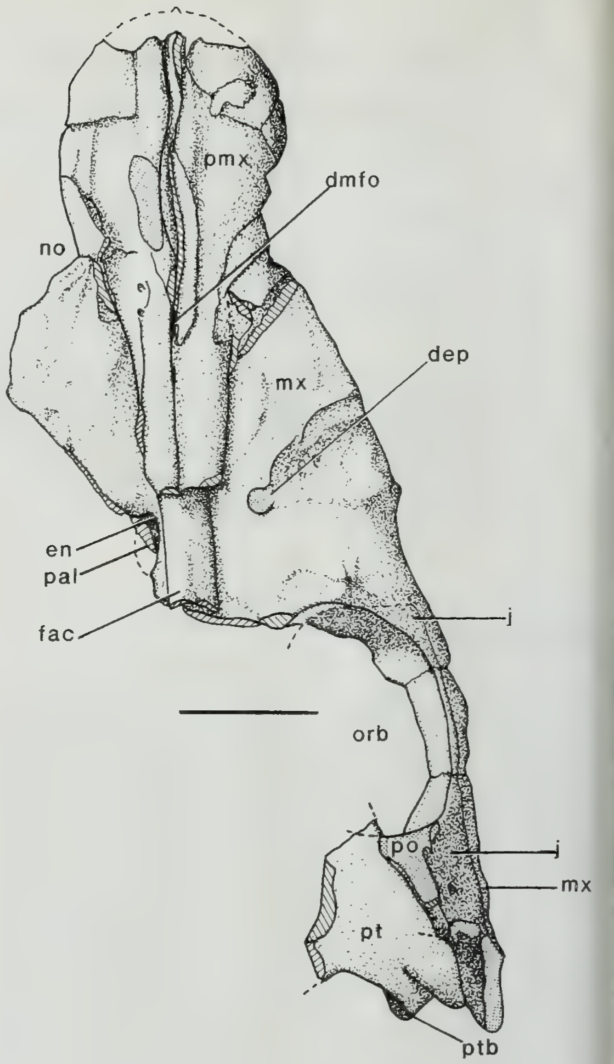

Fig. 1 *Rhomaleosaurus thorntoni* Andrews; dorsal view of the skull; scale bar = 100mm. For abbreviations on this and the other figures, see Table 1.

1994*a*), or indeed the Kimmeridgian species *Pliosaurus brachyspondylus* (Taylor & Cruickshank 1993*b*).

The anterior palatal surface shows much less damage. A very few fully erupted (mature) teeth are still in their sockets, but several replacement teeth are present, both in primary and secondary alveoli. The anteriormost edge of the anterior interpterygoid vacuity is visible, as is the lateral part of the outline of the right suborbital fenestra. The tooth sockets towards the rear of the maxilla become very indistinct and an accurate count is not possible, but at least 24 tooth positions can be identified, comprising five in each premaxilla plus 19 or 20 in the right maxilla.

Sutures between the individual bones of the palate cannot readily be distinguished except the premaxillae and maxillae. The vomers are substantial bones, forming a midline bar on the palate. Anteriorly they terminate in a horseshoe-shaped structure with several associated foramina. The vomers widen posteriorly, and are here flanked by grooves which run to the internal nares from fan-shaped areas just behind, and internal to, each diastema, opposite the notches where the premaxillae meet the maxillae. These fan-shaped areas are

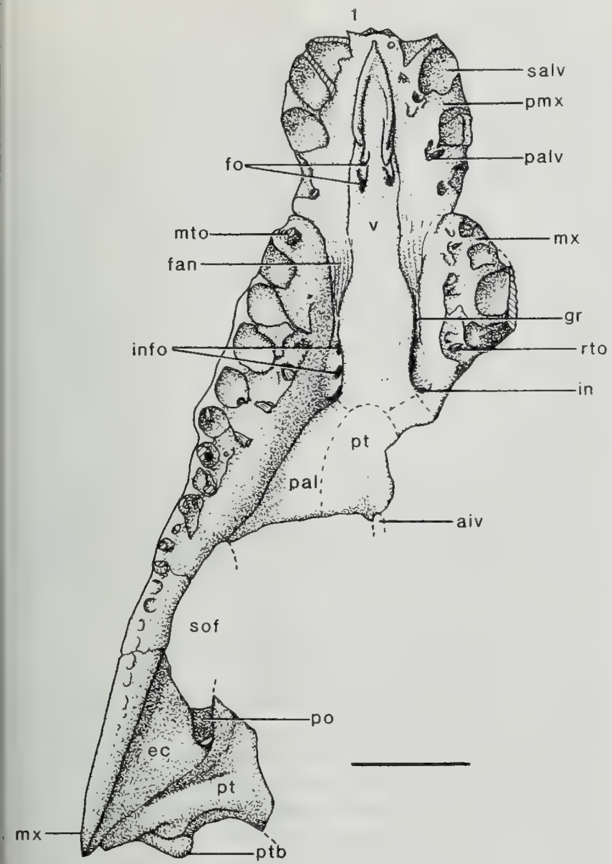

Fig. 2 *Rhomaleosaurus thorntoni* Andrews; ventral view of the skull; scale bar = 100 mm.

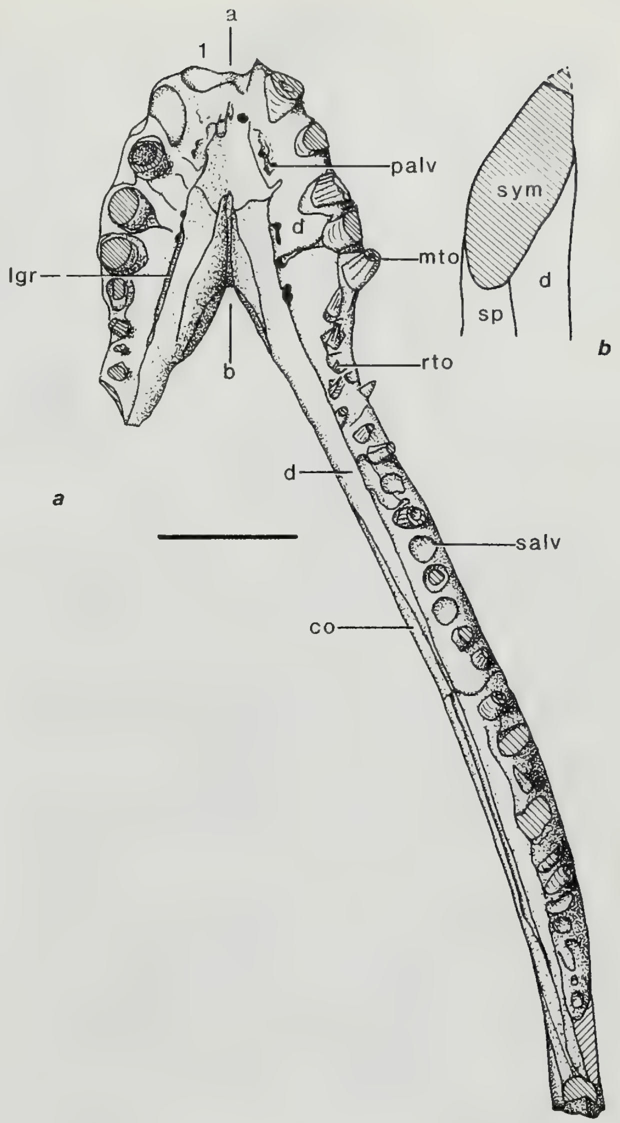

Fig. 3 *Rhomaleosaurus thorntoni* Andrews; lower jaw; **3a**, dorsal view; **3b**, section through symphysis on line *a–b*; scale bar = 100 mm.

covered in a radiating set of shallow grooves, suggesting that they helped anchor the buccal lining.

These features of the internal narial region are different from those of *Pliosaurus brachyspondylus* and *R. megacephalus*, where the structure is more fully known (Cruickshank *et al* 1991; Taylor & Cruickshank 1993*b*). In *P. brachyspondylus*, the internal nares lie at the end of grooves in the roof of the mouth, with two prominent foramina lying on the medial faces of the depression in front of each internal naris, all equally spaced. This is markedly different from *R. megacephalus*, where the internal nares lie at the ends of grooves, medial to, and parallel with, supplementary grooves which end in foramina. In neither of these species is there a fan-shaped area medial to the diastema, nor the extra foramina lying within the limits of the internal narial excavation, as illustrated here. As in all plesiosaurs which I have examined, the internal nares lie anterior to the external nares, inviting the explanation that the narial system acted as a hydrodynamically driven olfactory system, and was not used for respiration (Cruickshank *et al* 1991). The internal nares in *R. zetlandicus* and *R. cramptoni* are not visible, being obscured by the rami of the lower jaw (Taylor 1992*b*), or matrix.

The badly disrupted posterior palatal elements show that there was a prominent pterygoid boss in exactly the same position as in *R. zetlandicus* (Taylor 1992*a*; *b*), and an ectopterygoid lying between the jugal and pterygoid.

Mandible (Figs 3, 4). Parts of the lower jaw preserved include an almost complete right ramus as far back as the end of the dentary, the symphysis and the left ramus to just behind the symphysis, plus a portion of the middle of the left ramus and the left articular region (not illustrated). These portions of the lower jaw correspond almost exactly to the remains of the skull and no doubt represent what was saved during collection, from what must have been an almost complete cranium.

The symphysis occupies five tooth positions and a further 26 tooth positions can be counted in the right dentary. The general obscurity of sutures makes it difficult to identify individual bones, but as far as can be seen, the structure of this lower jaw is the same as that of *R. zetlandicus* (Taylor 1992*b*). There are both mature and replacement teeth present in the lower jaw, with their associated primary and secondary alveoli.

On the portion of the left jaw ramus containing the glenoid fossa, there is a large dorso-median trough on the prearticular and articular (Taylor 1992*b*: fig 7; Cruickshank 1994*a*: fig 7), which may be one of the determining characters of the genus *Rhomaleosaurus* (Taylor 1992*a*; Cruickshank 1994*a*).

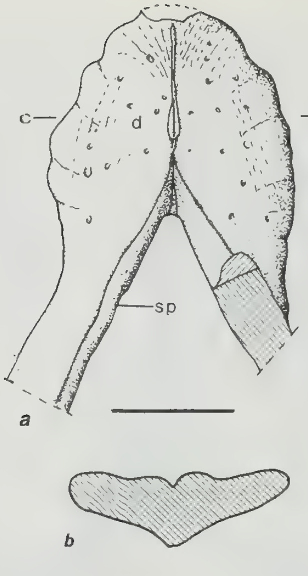

Fig. 4 *Rhomaleosaurus thorntoni* Andrews; symphysis of lower jaw; **4a**, ventral view; **4b**, section through symphysis on line *c–d*; scale bar = 100 mm.

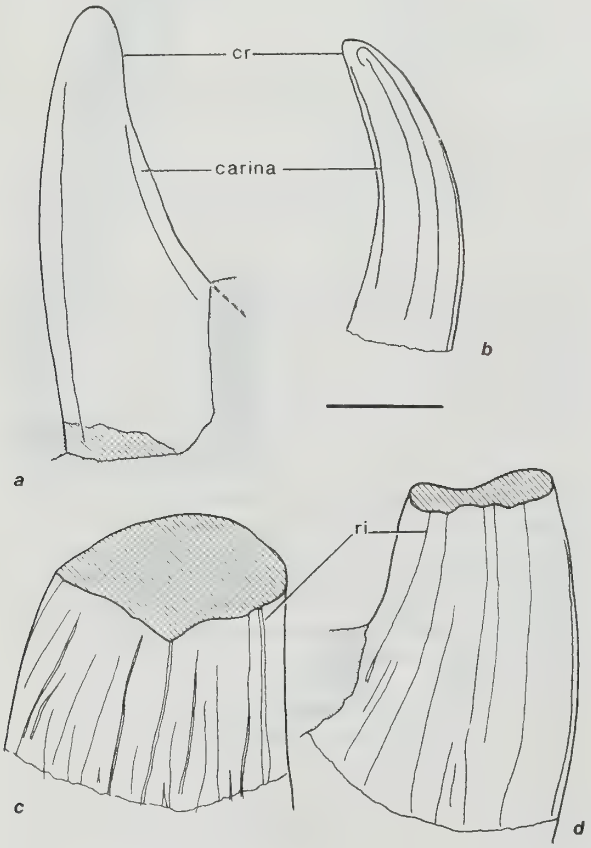

Fig. 5 *Rhomaleosaurus thorntoni* Andrews; teeth; **5a**, replacement tooth crown, position 9, right maxilla; **5b**, replacement tooth crown, position 24, right dentary; **5c**, mature tooth, position 12, right dentary; **5d**, mature tooth, position 8, right dentary; teeth are oriented with crowns towards top; drawn with an Abbé drawing apparatus on a Wild M3 stereomicroscope; scale bar = 5 mm.

Dentition (Fig. 5). The dentition is that of a powerful predator, with a rosette of interlocking, procumbent teeth in the premaxillae and lower jaw symphysis, followed by tooth-rows which, after two small median teeth, have large caniniforms in the upper jaw overlapping somewhat smaller teeth in the lower jaw. The tooth adjacent to the midline in both the upper and lower dentitions is much smaller than the more mesial teeth. In the lower jaw there is a marked reduction in size of teeth immediately behind the fifth position, which continues in a regular manner to the end of the tooth row on the dentary. In the upper jaw the fifth tooth position is very small, and is followed behind the diastema by another small tooth. Tooth positions seven, eight, nine and ten are very much larger caniniforms. Thereafter there is an even more marked reduction in tooth size, when compared with the lower dentition, until the sockets become difficult to distinguish. This arangement is very similar to that of *R. zetlandicus* (Taylor 1992*b*), allowing for the incompleteness of that specimen.

It is possible to amplify the description of the individual teeth offered by Taylor (1992*b*), for *R. zetlandicus*. Those illustrated come from the 9th position on the right maxilla, showing the buccal surface (Fig. 5*a*); lying across the root of the 23rd tooth on the right ramus of the lower jaw (Fig. 5*b*); the 12th position of the right ramus of the lower jaw (Fig. 5*c*); and the 8th position of the right ramus of the lower jaw (Fig. 5*d*). Figs 5*a* and 5*b* are replacement teeth, whereas Figs 5*c* and 5*d* are erupted, mature teeth.

The crowns are covered in a coarse ornament, which reduces in number of ridges towards the tooth-tip, but which all seem to have carinae on mesial and distal surfaces. The ornament on these teeth is identical with those illustrated by Taylor (1992*b*: fig. 9), but quite different from the tooth illustrated by Cruickshank (1994*a*: fig. 10) for *R. megacephalus*, where the ornament is much finer and more closely spaced. The ridges are triangular in section, and some start slightly below the crown–root boundary.

DISCUSSION

Andrews (1922: 413) compared *R. thorntoni* with *R. cramptoni*, regretting that the shoulder girdle of the latter was not visible and that he could not therefore use it for comparative taxonomic purposes. The skull and vertebral column of each species seemed to be much the same, but he drew attention to the following differences between them. Firstly, he thought that the external nasal openings were much further in front of the eyes in *R. thorntoni* than in *R. cramptoni*. Secondly, he recognized differences in the platforms of their cervical neural arches: in *R. thorntoni* these are nearly horizontal, but in *R. cramptoni* they are strongly inclined. Thirdly, he pointed out that the humerus in *R. thorntoni* was relatively larger, with a more expanded distal end.

Neither of the external nasal openings are very obvious in *R. thorntoni*: that on the right side is obscured by the displaced facial processes of the premaxillae, and that on the left is only partly preserved and probably invisible before the skull was recently cleaned properly. However, there is the depression some distance in front of the right orbit which could have been mistaken for an external naris prior to full cleaning of the specimen, and this would agree with Andrews' identification of an unusually anteriorly placed external nasal opening. This depression is floored with crushed bone, and does not penetrate onto the underside of the dermal bones of the snout. Restoration of the snout region (Fig. 6*c*) using information now available, shows the external nares to be situated in a normal position relative to the orbits.

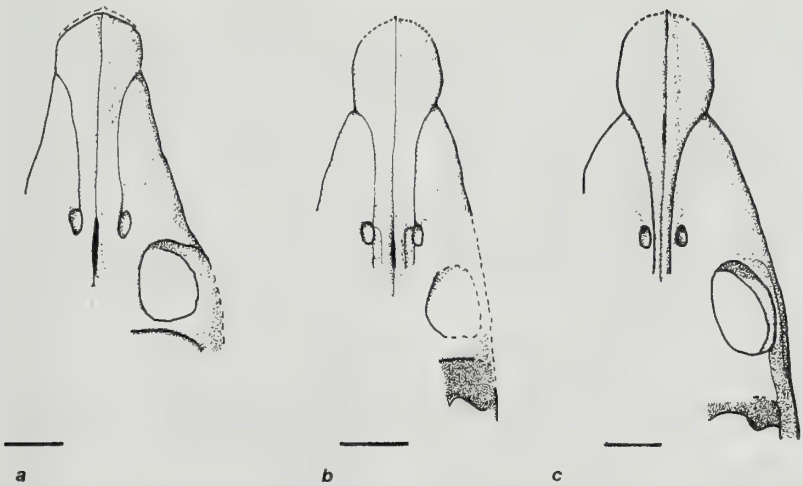

Fig. 6 Outline reconstructions of the anterior portion of skulls; **6a**, *Rhomaleosaurus cramptoni* (Carte & Baily, 1863), from a photograph of the type NMING F8785; **6b**, *Rhomaleosaurus zetlandicus* (Phillips, *in* Anon, 1854), after Taylor 1992*b*; **6c**, *Rhomaleosaurus thorntoni* Andrews, 1922; scale bars = 100 mm.

The differences in orientation of the zygapophyses in the cervical vertebrae of Plesiosauria depend on their relative position in the neck. In general the zygapophyses of the anterior cervical vertebrae are horizontally oriented, becoming inclined after the first ten or so. For instance in MANCH LL8004, a specimen of *Macroplata longirostris* (Blake) (Broadhurst & Duffy 1971), there are about 32 cervical vertebrae, of which the first ten have horizontal zygapophyses, while the remainder have zygapophyses angled at about 45° to the horizontal. Liassic plesiosaurs in general seem to have between 28 and 32 cervical vertebrae. Even in the posteriormost cervicals, the rib articulations are placed close to the lower rim of the centra (Taylor & Cruickshank 1993*a*), and therefore could still appear to be from a more anterior position. Therefore, it is not always obvious from which part of the neck any single vertebra might come, and hence to draw conclusions about zygapophyseal orientation is premature.

The question of the characters of the humeri may well depend on the state of preservation of each. The skull and skeleton of *R. cramptoni* are very much less damaged than those of *R. thorntoni*, and it seems unwise to make strict taxonomic statements on this character without knowing more about individual variation within the genus *Rhomaleosaurus*.

Therefore, the principal points of difference between the two species can be interpreted as being due to either their relative state of preservation, their size, or to an unreliable character, as in the case of the neck vertebrae. On the basis of the foregoing discussion, both *R. cramptoni* and *R. thorntoni* are seen to belong to the same species. In addition they come from approximately the same horizon, in the Toarcian stage of the Liassic (Lower Jurassic) of England.

One other similar pliosauroid is known from the Yorkshire (England) Toarcian, *R. zetlandicus* (Phillips, *in* Anon, 1854) (Taylor 1992*a*). Reconstructions of part of the skulls of *R. thorntoni*, *R. zetlandicus* and *R. cramptoni* are shown for comparison (Figs 6*a*–*c*). The relevant differences lie in the overall size of each and in the apparent width of the postorbital bar; in *R. thorntoni* it is relatively wider than in *R. zetlandicus* and *R. cramptoni*, but as all specimens are variously damaged in that area, no firm conclusions can be reached on this character. All specimens have the same short, broad snout, which contrasts with the more slender, relatively longer snout of the Hettangian *R. megacephalus* (LEICS G221.1851) (Cruickshank 1994*a*). The Toarcian specimens have similar dentition, possessing sparsely ridged teeth, which also contrasts with those of *R. megacephalus*.

Taking all three Toarcian species together (Fig. 6), it is probable that they represent only size variants of the same species. They are conspecific and should be referred to the single species *Rhomaleosaurus zetlandicus* (Phillips, *in* Anon, 1854), which has date priority.

In Fig. 6, which compares that part of the skull preserved in R4853 with the other two types, it will be noted that the premaxillaries of R4853 are apparently narrower than those of the other two specimens. The reconstruction was effected using the most conservative measurements, and perhaps this is reflected in a false narrowing of the premaxillary facial processes. It is not likely that, for instance, any conclusions can be drawn from such a reconstruction concerning growth rates, or sexual dimorphism.

SUMMARY AND CONCLUSIONS

1 The skull of the type specimen of *Rhomaleosaurus thorntoni* Andrews, 1922, from the Toarcian of Northamptonshire, is illustrated for the first time. Additional information concerning details of its external nares, and reassessment of other characters discussed in the original description, make it difficult to sustain its supposed differences from *R. cramptoni* (Carte & Baily, 1863) from the Toarcian of Yorkshire.
2 Comparisons with the type of *R. zetlandicus* (Phillips, *in* Anon, 1854), also from the Toarcian of Yorkshire, indicate that *R. thorntoni* is merely a larger specimen of *R. zetlandicus*.
3 Since all three specimens are shown here to belong to the same species, the correct name for it is *Rhomaleosaurus zetlandicus* (Phillips, *in* Anon, 1854).
4 *Rhomaleosaurus zetlandicus* was the top predator in the Upper Lias of England. *R. megacephalus* from the Rhaetian or Hettangian (Lower Lias) has a longer, more slender snout, and different dentition.

Acknowledgements. The type of *Rhomaleosaurus thorntoni* was cleaned at the Natural History Museum, London, under the direction of Dr Angela Milner, at the request of Dr Michael Taylor. I am grateful to Dr Milner for the loan of this specimen, and for access to the mounted cast of the type of *R. cramptoni* (BMNH R34) in the Natural History Museum, and to Dr Taylor for discussion and access to his collection of reference slides. Mr John Martin, Keeper of Earth Sciences, and the Director of the Leicestershire Museums Service provided facilities for the work to be undertaken. The assistance of Mrs Anne Montgomery of the Geology Department, University of Leicester is gratefully acknowledged. Mr Nigel Monaghan (NMING) cheerfully supplied photographs of the type of *R. cramptoni*. John Martin, David Brown, Angela Milner and Michael Taylor read drafts of the manuscript, to its great improvement. The work was done during the tenure of a Leverhulme Fellowship awarded to Dr M A Taylor.

REFERENCES

Andrews, C. W. 1922. Notes on the skeleton of a large plesiosaur (*Rhomaleosaurus thorntoni* sp.n) from the Upper Lias of Northamptonshire. *Annals and Magazine of Natural History*, **9**, **10**: 407–415.

Anon 1854. Report of the Council of the Yorkshire Philosophical Society. *Annual Report of the Yorkshire Philosophical Society for 1853*: **7, 8.**

Benton, M. J. & Taylor, M.A. 1984. Marine reptiles from the Upper Lias (Lower Toarcian, Lower Jurassic) of the Yorkshire coast. *Proceedings of the Yorkshire Geological Society*, **44**: 399–429.

Broadhurst, F. M. & Duffy, L. 1971. A plesiosaur in the Geology Department, University of Manchester. *Museums Journal*, **70**: 30–31.

Brown, D. S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum (Natural History), (Geology Series)*, **35**: 253–347.

Carte, A. & Baily, W. H. 1863. Description of a new species of *Plesiosaurus* from the Lias, near Whitby, Yorkshire. *Journal of the Royal Dublin Society*, **4**: 160–170.

Cruickshank, A. R. I. 1994*a*. Cranial anatomy of the Lower Jurassic pliosaur *Rhomaleosaurus megacephalus* (Stutchbury) (Reptilia; Plesiosauria). *Philosophical Transactions of the Royal Society of London*, (B) **343**: 247–260.

—— 1994*b*. A juvenile plesiosaur (Plesiosauria: Reptilia) from the Lower Lias (Hettangian: Lower Jurassic) of Lyme Regis, England: a pliosauroid – plesiosauroid intermediate? *Zoological Journal of the Linnean Society of London*, **112**: 151–178.

——, **Small, P. G. & Taylor, M. A.** 1991. Dorsal nostrils and hydrodynamically driven underwater olfaction. *Nature*, London, **352**: 62–64.

Phillips, J. 1854. On a new *Plesiosaurus* in the York Museum. *Annual Report of the British Association for the Advancement of Science for 1853*, 54.

Stutchbury, S. 1846. Description of a new species of *Plesiosaurus* in the Museum of the Bristol Institution. *Quarterly Journal of the Geological Society of London*, **2**: 411–417.

Taylor, M. A. 1992*a*. Taxonomy and taphonomy of *Rhomaleosaurus zetlandicus* (Plesiosauria; Reptilia) from the Toarcian (Lower Jurassic) of the Yorkshire coast. *Proceedings of the Yorkshire Geological Society*, **49**: 49–55.

—— 1992*b*. Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria; Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire. *Philosophical Transactions of the Royal Society of London.*, (B) **335**: 247–280.

—— **& Cruickshank, A. R. I.** 1989. The Barrow Kipper, *'Plesiosaurus' megacephalus* (Plesiosauria; Reptilia) from the Lower Lias (Lower Jurassic) of Barrow upon Soar, Leicestershire. *Transactions of the Leicester Literary & Philosophical Society*, **83**: 20–24.

—— **&** —— 1993*a*. A plesiosaurian reptile from the Linksfield erratic (Rhaetian; Upper Triassic) of Morayshire. *Scottish Journal of Geology*, **29**: 191–196.

—— **&** —— 1993*b* Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia; Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire. *Philosophical Transactions of the Royal Society of London*, (B) **341**: 399–418.